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A CONSIDERATION OF THE CHEMICAL BASIS OF FOOD PREFERENCE IN MILLIPEDES

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SYNOPSIS

The acceptance of decomposing materials by millipedes correlates with the nitrogen content, the carbohydrate content and the moisture content. The microbiota act to release available food substances and to decrease the polyphenol and tannin concentration. It is suggested that the release of simple sugars from complexes and polyoses serves to increase the palatability of litter leaves and also to act as an index for the nutritiveness of the food. The polyphenol and tannin content of the leaves oppose the effect of sugars upon palatability.

INTRODUCTION

Feeding preference

It has been postulated by Dethier (1937) and Thorsteinson (1953a quoted by Dadd, 1963) that the preference of insects for food plants depends upon the presence of common specific substances which provide olfactory or gustatory stimuli without which feeding fails to occur. Thorsteinson (1960 quoted by Dadd, 1963) however suggests that while feeding is primarily stimulated by universally distributed food substances, including both nutrients and water, various degrees of oligophagy result from the presence of factors which inhibit feeding. Thus food preference involves a balance between acceptance and rejection.

Many authors (Schmidt, 1952; Barlow, 1957; van der Drift, 1965) have shown that millipedes exhibit preferences in their choice of food. They have also shown that the most preferred food varies with the species of millipede under consideration although this preference may be masked by a need on the part of the millipede for a variety of foodstuffs. Schmidt (1952) notes that the inter-specific differences in food preference allow of a maximal transformation of available foods.

Physical and chemical features of preference

Although many authors have attempted to isolate the factors involved in millipede food preferences, it has only been possible to correlate chemical and physical factors of the food with its palatability, without isolating the causative factor.

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Lyford (1943) working with *Diploiulus londinensis* found a correlation between the calcium content of litter leaves and the preference of the millipede. He concluded that leaf species was the important factor in determining the millipede's preference.

Murphy (1953), however, found that the calcium content was inversely related to the carbon : nitrogen (C : N) ratio, while Wittich (1943, 1953) found that the C : N ratio was the controlling factor in determining the rate of decomposition of leaf litter. He determined also that the nitrogen rich leaves were the most readily consumed.

Bocock (1964) found that the nitrogen content of litter increases with its age, and this can be correlated with Kheirallah's (1966) finding that the palatability of leaves increases with age. Similarly Schmidt (1952) established that the palatability of different species of dead leaves depended not only upon the species but upon the age of the leaf.

Dünger (1958) in his examination of the effects of mechanical features of leaves found that these were of little significance with regard to palatibility although Barlow (1957) points out that a certain degree of softness is required to overcome the limitations of the chewing mechanism of millipedes.

Both Dünger and Barlow feel that the moisture content is important although not the limiting factor. This is of interest since Brade-Birks (1930) observed that millipedes will eat a great variety of substances and suggested that they do this for the sake of the moisture they can obtain.

Cloudsley-Thompson (1951) postulates that millipedes attack crop plants during periods of drought for the sake of moisture. He also hypothesizes that the sugars present in the sap restrain the millipedes from returning to their normal diet thus exacerbating the severity of damage.

In his view the attractive properties of rotting substances are due only to sugars, provided that suitable contact and moisture stimuli are present. Thorsteinson (1958a quoted in Dadd, 1963) also notes that the presence of sugar commonly induces insects to feed.

We thus find that three main features of the litter leaf have been correlated with acceptance by the millipede, viz:—nitrogen content, sugars, and moisture.

The role of the microbiota

The increase in palatability of leaves with age has been explained by several authors in terms of a decrease in the concentration of a rejection factor. For example Edwards in Minderman & Daniels (1967) suggests that this is brought about by the leaching of water soluble polyphenols from the leaf.

Satchell & Lowe (1967) found a strong relationship between the polyphenol content of leaves and their palatability to *Lumbricus terrestris* but Thiele (1959) found that soaking leaves in a 2% tannin solution did not affect their palatability to millipedes. He did however find that fresh litter was rejected while litter weathered for a year was acceptable.

Other workers have attempted to explain the changes in palatability with age of litter leaves by implicating the microbiota in the breakdown of the water soluble polyphenols and of the cell contents in general. Minderman & Daniels (1967) found that newly fallen leaves had little attraction for most litter-eating animals but that leaves which had been lying on the ground for some time were readily consumed. These authors suggest that a certain concentration of bacteria and fungi has to develop in the litter before it becomes palatable. The microflora is seen as the most important source of nutriment for the litter eaters with the leaf tissue acting mainly as a sub-stratum.

Saudray (1961) also found that the nutritive value of the food eaten depends upon the extent of its alteration by fungi and bacteria both of which increase the amount of lipid, carbohydrate, and protein.

A major insight into the role of the microbiota can be derived from Handley's (1954) finding that the cell contents of litter leaves are combined into protein complexes which vary in the ease of their decomposition. The function of the microbiota is to render the cell contents accessible to the litter eaters by incorporating these complexes into their own substance. Minderman & Daniels (1967) point out that bacterial and fungal protein is more readily available to the fauna than the residual leaf protein. Similarly Striganova (1967) concludes that the decomposition of leaf litter is a microbial opening-up of the food and that the rate of this is dependent upon the structural properties of the species of leaf.

The importance of this can be gauged from the finding of Gere (1956) that the amount of litter consumed by millipedes and the amount utilized depends upon its state of decomposition when eaten. Millipedes eat more and use less of undecomposed material. Schmidt (1952) also found an intimate relationship between the extent of decomposition and the uptake of litter leaves, and concludes that the determinant of choice is unquestionably the degree of decomposition.

Further evidence for this view comes from Nielsen's (1962) finding that microbial enzyme systems are much more efficient than the enzymes of other invertebrates in the decomposition of the structural polysaccharides of leaves. Thus he envisaged the primary decomposition of litter leaves as being due to the microbiota. This was supported by

his finding that there is a poor correlation between the type of diet and the carbohydrases present in a range of litter eating animals.

Although Brade-Birks (1930) suggested that millipedes do not discriminate on a chemical basis in their choice of food substances, Kheirallah (1966) was able to show that the quantity of food eaten depends upon its nutritive value. Larger amounts of the less nutritive substances were eaten if the animal was offered no choice.

Millipedes are therefore able to assess the nutritive value of their food and this may be related to the palatability. The palatability may depend on the presence of rejection and/or acceptance factors.

It is conceivable that the food of the litter feeding millipedes has little attraction when fresh owing to the presence of inhibitory factors (perhaps the polyphenols and tannins). It may become more palatable as a result of the microbial activity in reducing these factors, and also because of an increase in the concentration of attractive factors (perhaps available food substances).

Since sugars commonly induce feeding in insects (Dadd, 1963) the work in this paper has been directed at elucidating the response of millipedes to various carbohydrates. An attempt has also been made to discover the role of polyphenols and tannins in affecting palatability.

Materials and methods

The organisms studied were *Tachypodoiulus niger* (Leach 1815), *Ommatoiulus sabulosus* (Linné 1758), *Polymicrodon polydesmoides* (Leach 1815), *Polydesmus angustus* Latzel 1884, and *Glomeris marginata* (Villers 1789), collected from sycamore woods (*Acer pseudoplatanus*) in Derbyshire.

BEHAVIOURAL EXPERIMENTS

Establishment of scale of choice

The assessment of the response of millipedes to a dissolved substance is difficult because of the absence of an easily quantifiable response. It is not possible to observe the extrusion or unrolling of the mouthparts as used by Minnich (1921, 1926), Mcindoo (1934), Dethier & Wolbarsht (1956), and Hodgson (1957) for the "haustellate" insects. Nor is it possible to employ the "biting" response used by Thorpe, Crombie, Hill & Darrah (1947) for wireworms since the weak mouthparts of millipedes cannot mark filter paper (Cloudsley-Thompson, 1951).

Because of the absence of a suitable method for estimating the feeding response it is not possible to assess the feeding responses separately from the orientating responses. As a result the technique

finally evolved measured a combination of the orientation responses and the feeding responses. This was a preference experiment based on the techniques used by Wigglesworth (1941), Thorpe *et al.* (1947), Cloudsley-Thompson (1951), Brookes (1963), and Fairhurst (1968).

Methods

Initially the apparatus used was that of Fairhurst after Brookes using a substrate of air dried peat after Cloudsley-Thompson. This substrate was however found to be unsuitable since the animals tended to burrow into the peat. This was perhaps a light avoidance reaction or more probably a response to the strong thigmotaxis which millipedes exhibit (Crozier & Moore, 1923). To avoid these effects, a 14 cm diam. glass Petri dish, with a low central partition of celluloid, was substituted. The substrate employed was Whatman No. 1 filter paper.

This apparatus was easy to clean between experiments and also avoided the various apparatus effects enumerated by Graham & Waterhouse (1964). Thus end and corner effects were obviated by using round dishes to prevent the collection of millipedes in corners in their efforts to maximize tactile stimulation.

Preliminary experiments were performed to detect and avoid the influence of external effects upon the apparatus and also to determine the optimal time for the experiments. Dadd (1963) suggests that insects respond to feeding stimuli only when hungry, and accordingly various periods without food were tried to obtain a consistent response. Twenty four hours' starvation on moist cotton wool prior to the experiment was found to be sufficient.

A block of 12 of these modified Petri dishes was set up, according to a random selection procedure, with de-ionized water moistened filter paper on one side and filter paper moistened with test solution on the other side. Six starved animals were introduced into each dish and their position was noted at two-minute intervals for 20 min.

A statistical analysis (Anovar) justified summing the replicates. These totals were then represented graphically and the concentration at which the behavioural response became significant at the 5% level (obtained by means of the Chi squared test) was taken to be the behavioural threshold for that substance (see Table I).

Rationale

Cloudsley-Thompson (1951) concluded from his experiments that the response of millipedes to contact chemical stimuli was purely orthokinetic. He also found no evidence for a "biting" response as distinct from an "orientating "response.

TABLE I

Threshold of behavioural preference as compared to water

Substance	*T. niger*	*O. sabulosus*	*P. polydesmoides*	*P. angustus*	*G. marginata*
D(+)Glucose	0·0970	0·0555	0·1645	0·1460	0·1645
D(−)Fructose	0·0925	0·0535	0·0843	0·0936	0·075
D(+)Galactose	Not significant	Not significant	Not significant	Not significant	Aversive
D(+)Mannose	Aversive	Not significant	Not significant	Not significant	Not significant
L(−)Sorbose	0·25	0·39	0·675	—	0·265
D(+)Xylose	0·655	0·28	Not significant	—	Not significant
D(−)Arabinose	Not significant	Aversive	Aversive	—	Aversive
Sucrose	0·0135	0·013	0·076	0·0634	0·074
Maltose	0·00995	0·00595	0·02	0·029	0·0425
Lactose	Not significant	Not significant	Not significant	Not significant	Not significant
Mannitol	Aversive	Not significant	Not significant	Aversive	Not significant
D(+)Glucosamine hydrochloride	Not significant	Aversive	Aversive	Aversive	Not significant
Sodium chloride	Aversive 0·855	Aversive 0·0825	Aversive 0·072	Aversive 0·081	Not significant
Potassium nitrate	Aversive 0·18	Aversive 0·11	Aversive 0·0755	Aversive 0·0046	Aversive 0·088

Concentration in moles per litre.

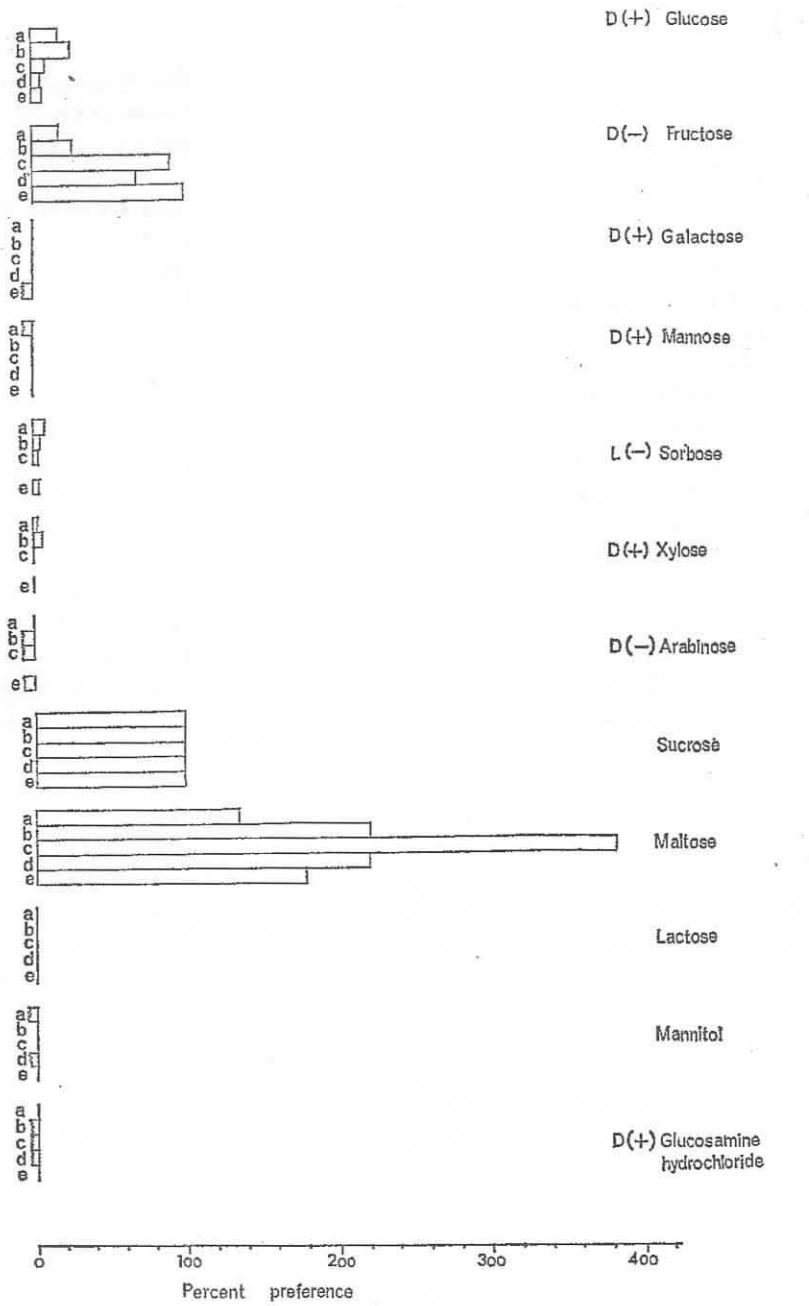

FIG. 1. Comparative behavioural preference to sugar. The histograms represent the preference of five species for a series of sugars compared with sucrose at 100%. The five species against each sugar are, from top to bottom, a–e:
Tachypodoiulus niger, *Ommatoiulus sabulosus*, *Polymicrodon polydesmoides*, *Polydesmus angustus*, and *Glomeris marginata*.

Kheirallah (1966) demonstrated that millipedes respond to food substances by searching until a suitable food substance is found, when feeding supervenes. This is interrupted before satiety by a further bout of searching behaviour.

As a result of either this theory or of the orthokinetic theory describing the behavioural response to gustatory stimuli it may be deduced that the animal will spend more time on the preferred side of the dish than on the less preferred side. This will be reflected by the position records (Fig. 1).

An interesting observation during these experiments was the continual tapping of the substrate by the antennae during locomotion. This seemed to be a sampling procedure whereby the antennal tips were applied to the substrate in front of and to the sides of the animal. Occasionally an animal upon crossing the boundary from sugar to water stopped and tapped with its antennae until it re-encountered sugar solution when it returned to the sugar sector.

The rationale behind the experimental procedure is that measurements based upon the reactions of an entire animal may be used to estimate the sensitivity of the animal's receptors (Hodgson, 1953). The possibilities for error are clear but the validity of the measurement is suggested in view of the generalization from comparative psychology that the correlation between the structure of the nervous system and the behaviour of an animal becomes clearer as one considers experimental material along phyletic lines from mammals down through the invertebrates (Schneirla, 1952, in Hodgson, 1953).

Dethier & Chadwick (1948) have shown, for insect chemoreception, the excellent correlation between known physical and chemical properties of stimulating compounds and the thresholds for behavioural response to them. This suggests that there are no unknown factors in the nervous system which would prevent such clear correlations by modifying the consistent relation between the properties of the stimulus applied and the whole animal's reaction.

Thus it appears that the behavioural response of a lower organism to an applied stimulus is a fair measure of the comparative stimulating ability of that stimulus.

ANALYSIS OF LEAF LITTER

In an attempt to determine the relevance of these behavioural responses to the normal life of the millipedes the sycamore (*Acer pseudoplatanus*) leaf litter which they inhabited was analysed using thin layer chromatography to identify the sugars present. Colorimetric

methods were used to assess quantitatively the simple carbohydrate and the glucose present. Behavioural responses to fractions of the leaf extracts were also determined.

Methods of analysis of litter leaf extract

Extraction

The laminae of freshly collected litter leaves were blended in 80% ethanol and this extract was left overnight at 60°C to ensure dissolution of the carbohydrates. The insoluble material was then removed by vacuum filtration. This solvent extracts only low molecular weight carbohydrates up to, at most, pentasaccharides (H. E. Grant pers. comm.), thus it does not extract starch or hemicellulose.

This alcoholic solution was then evaporated to dryness under reduced pressure at less than 60°C and the residue was taken up in de-ionized water. This solution was then decolorized by shaking with diethyl ether followed by ethyl acetate to remove lipids, polyphenols, and tannins.

Total carbohydrate assay

Three ml of chilled freshly prepared orcinol reagent were thoroughly mixed with 1 ml of the litter extract. The mixture was then heated on a water bath at 100°C for 10 min to develop the orange/yellow colour reaction. The solution was then cooled to 5°C and the absorption of light at 500 mμ was determined. The concentration of carbohydrate present was found from a reference graph calibrated from solutions containing 0 to 25 μg/ml of glucose. The results were expressed in terms of the quantity of carbohydrate obtained from 100 g dry weight of leaf laminae (Fig. 2).

Glucose assay

The glucose content of the litter extract was assayed using Modder's (1965) method, although the trichloro acetic acid was omitted since no protein or enzymes were present. This avoids the possibility of hydrolysis of the relatively unstable disaccharides such as sucrose or maltose (Schmidt, 1955).

The glucose concentration was obtained from a reference graph calibrated for glucose standard solutions containing 5–25 mg/l of glucose in deionized water. The concentration of glucose was expressed in g/100 g dry weight of leaf laminae (Fig. 2).

Thin-layer chromatography

The remaining extract was de-ionized and the eluent reduced in volume to about 20 ml at reduced pressure. Two ml of *n*-propanol was

added to prevent fungal and bacterial growth allowing of storage for a few days at 0°C.

The method used was derived from Stahl (1965). Inactive Kieselgel G plates 50 microns in depth were used together with methyl ethyl

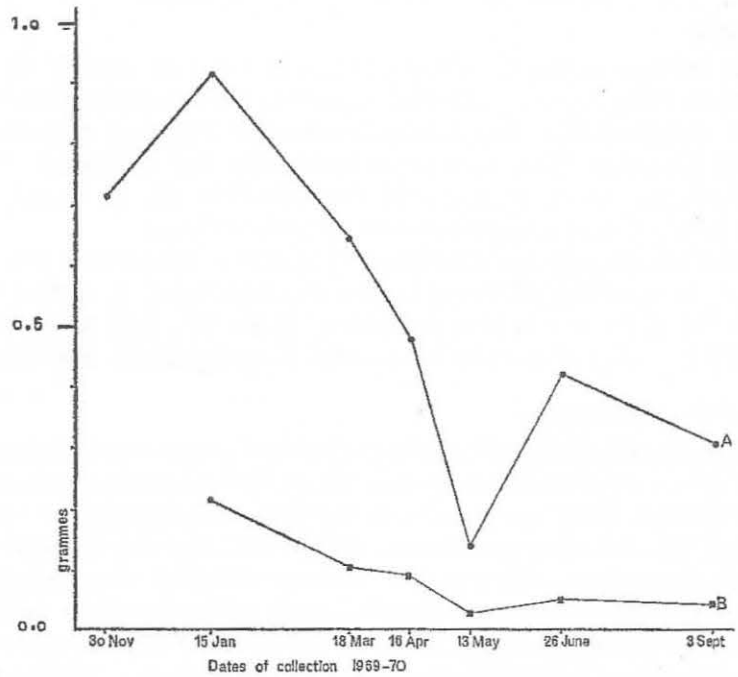

FIG. 2. Analysis of sycamore litter extract. Dry weight in g of (A) total carbohydrate and (B) glucose; both in 100 g dry weight of litter.

ketone, acetic acid (glacial) and methanol 6 : 2 : 2 as the solvent. The plates were developed with either aniline hydrogen phthallate or anisaldehyde. The Rf values were calculated for the test and reference spots and in this way the unknown sugars were identified (Table II).

Plates were also run at right angles with a second solvent, (two-dimensional chromatography), *n*-butanol, acetone, water 4 : 5 : 1 to produce a greater separation, especially of glucose and fructose, thus permitting a more accurate characterization of the sugars.

Behavioural response to fractions of extract

Since it was thought that the polyphenol and tannin content of litter leaves plays a part in determining their palatability the behavioural responses of millipedes to these substances were assessed.

TABLE II

Qualitative analysis of sycamore litter leaf extract

Date collected	Sugars present in extract					
30–11–1969	Glucose	Xylose	Rhamnose			
15–1–1970	Glucose	Xylose	Rhamnose	Raffinose		
18–3–1970	Glucose	Xylose		Raffinose	Trehalose	Arabinose
16–4–1970	Glucose	Xylose	Rhamnose	Raffinose	Trehalose	Galactose
13–5–1970	Glucose	Xylose	Rhamnose	Raffinose	Trehalose	Arabinose
26–6–1970	Glucose	Xylose	Rhamnose		Trehalose	
3–9–1970	Glucose	Xylose	Rhamnose	Raffinose	Trehalose	

Three fractions were obtained from the litter leaf extract.

1. An ethereal fraction containing lipids and certain polyphenols.
2. An ethyl acetate fraction containing other polyphenols and tannins.
3. The remaining alcoholic solution containing the carbohydrates.

These were applied to filter paper and all traces of organic solvent were removed. The papers were then moistened with de-ionized water and were tested for preference against de-ionized water as in the previous behavioural experiments. The alcoholic fraction was also compared against the ether fraction and against the ethyl acetate fraction (Table III).

DISCUSSION OF RESULTS

There is a general preference for glucose, fructose, sucrose, maltose, and sorbose compared to water while *T. niger* and *O. sabulosus* also show a preference for xylose. Galactose, mannose, D(-) arabinose, lactose, mannitol, and D(+) glucosamine hydrochloride were either avoided or gave no differential response. The results, showing avoidance of sodium chloride and potassium nitrate, indicate that the responses to sugars are not due solely to osmotic conditions (Table I).

Thus those sugars found by Hassett, Dethier & Fans (1950), Nielsen (1962) and Wyatt (1967) to be the ones most likely to be nutritive and utilizable were also the ones to which these millipedes showed the greatest preference. A correlation seems to exist between the sugars found in the leaves and those most preferred. Haslinger (1935) suggests that substances without nutritive value are tasteless while those with a nutritive value may or may not be tasted. It therefore seems likely that the palatability of sugars may be an index to their nutritive value and since sugars commonly induce feeding this may be an index to the nutritive value of the litter leaf.

There is a strong correlation between the sugars found in the leaf litter extract and those found by Roelofson (1959) to be the main components of the plant cell wall (the major part of the litter leaf). He found the following carbohydrates:

1. Cellulose.
2. Lignin.
3. Hemicelluloses containing in complexes and polyoses; *d*-mannose, *d*-glucose, *d*-galactose, *d*-xylose, *d*-arabinose, and *l*-rhamnose.

These are similar to the ones which Mehta, Duboch & Deuel (1961) found in the soil. Mannose, however, was absent in the present work

TABLE III

Behavioural response to fractions of sycamore litter leaf extract

	Control water/water	Ethereal/ water	Ethyl acetate/ water	Alcoholic/ water	Alcoholic/ ethereal	Alcoholic/ ethyl acetate
T. niger	88/92	97/83	89/91	96/84	83/97	119*/61
O. sabulosus	95/85	92/88	92/88	94/86	108*/72	87/93
P. polydesmoides	86/94	90/90	83/97	93/87	90/90	84/96
P. angustus	94/86	97/83	96/84	96/84	104*/76	120*/60
G. marginata	88/92	91/89	86/94	93/87	108*/72	88/92

Ethereal fraction contains phenols.
Ethyl acetate fraction contains phenols and tannins.
Alcoholic fraction contains sugars.

* = significant, $p < 0{\cdot}05$.
Expected ratio for chi-square = 90/90.
5% range = 103/77.

from the extract and the trehalose found was probably derived from fungi (Nielsen, 1962).

Nielsen (1962) found that these complexes and polyoses of the plant cell wall are much more commonly hydrolysed by bacteria, fungi, and the lower herbivorous animals than are cellulose or chitin. He found that the enzymes required for the primary decomposition of litter were found mainly in the soil protozoa, snails, slugs, and in *Polydesmus*. However *Glomeris* which lacked the enzymes for primary decomposition was able to utilize the products of this decomposition, unlike *Polydesmus*.

The results from the behavioural tests with the three litter fractions are difficult to explain since none of the fractions gives a significant response when compared to de-ionized water, although there is a consistent but slight preference for the alcoholic (sugar containing) fraction (Table III). However, when the alcoholic fraction is compared to the diethyl ether fraction (containing lipids and polyphenol) *O. sabulosus*, *P. angustus* and *G. marginata* show a significant preference for the alcoholic fraction. In the case of a comparison between the alcoholic fraction and the ethyl acetate fraction (polyphenol and tannin), *T. niger* and *P. angustus* show a marked preference for the alcoholic fraction.

Thus there would seem to be some support for the view that polyphenols and tannins have an opposite effect on palatability to carbohydrates. Leaves which have a high content of polyphenols and tannin, and yet have not been subjected to the microbial action that increases the level of available carbohydrate, will be less palatable.

A preference for the alcoholic fraction over the ethereal fraction and over the ethyl-acetate fraction is not shown by *Polymicrodon polydesmoides*. However, this is a species which is found in large numbers in autumn, winter and spring when the sycamore leaves would be relatively undecomposed. It is therefore not surprising that phenol and tannin have less effect on it than on the other species.

As a result of the two factors of the primary decomposition of litter by the microflora and the need for common specific stimuli it is possible to advance an explanation for the variation of the palatability of litter leaves with age. Thus Kheirallah (1966) found that *Iulus scandinavius* rejected fresh sycamore leaves but that these became palatable after one month. The palatability then decreased over the next four months and then increased again until they were 14 months old.

This may be a result of the activity of the soil microbiota since Saudray (1961) postulated that the nutritive value of the litter depended upon the extent of its alteration by fungi and bacteria.

However a simple increase in the amount of available food substance is insufficient to explain Kheirallah's findings since they do not correlate

with the carbohydrate and glucose content from my analysis. The increased carbohydrate in June could be due to the fall of green plant material and of insect frass (Bocock, 1964), especially since the sycamore trees later developed a very high aphid population, but it could also be the result of increased temperature affecting microbial activity.

Although Thiele (1959) was unable to make litter leaves less palatable to Diplopoda by soaking them in tannin, Satchell & Lowe (1967) found a strong relationship between the polyphenol content of leaves and their palatability, for *Lumbricus terrestris*. They also found a rapid loss of polyphenol in the first six weeks of weathering which they explained as a result of microbial action. This loss of polyphenol could explain the increase of palatability of fallen sycamore leaves over the first month in Kheirallah's work.

CONCLUSION

It is probable that the palatability of the sycamore leaves is dependent upon the microfloral activity since Schmidt (1952) finds that food selection is unquestionably determined by the degree of decomposition of the food material. The microflora may act either by decreasing the polyphenol content, by increasing the amounts of nutritive substances or by both of these processes. The palatability should then correlate with environmental conditions since these affect the microbial activity.

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Discussion

Sundara Rajulu: You have suggested that the sugars present in the leaves are the phagostimulants, but Lyford (1943)* reported that calcium salts were the phagostimulants.

Sakwa: I have mentioned that the rate of decomposition of leaves depends on a low C : N ratio, which according to Murphy (1953)* is inversely related to the calcium content. It is probably more meaningful to refer the higher palatability to this low C : N ratio rather than to the calcium content.

Gabbutt: Does degradation result in an increased carbohydrate content?

Sakwa: Yes, according to Saudray, 1961*.

Gabbutt: But your graph showed a decrease later on, didn't it?

* See list of references, p. 344.

SAKWA: In Fig. 2 the first point on the graph (November) may represent the original quantity of carbohydrate present. The level drops overwinter, perhaps because of a lower microbial activity, and it then rises again during May, perhaps because of higher temperatures.

GABBUTT: The fall in the curve would then represent a loss of the originally present carbohydrate before degradation gets under way.

SAKWA: I would think so, but since I didn't analyse the leaves immediately after leaf fall—some degradation may have occurred before the first point on Fig. 2—the initial carbohydrate content may conceivably have been even lower than this.

GABBUTT: But that would suggest that the degradative processes produce only half as much carbohydrate again as was present at leaf fall.

SAKWA: Since I do not know precisely how much was originally present I cannot say.

GABBUTT: But 30th November is not long after leaf fall.

SAKWA: Yes, but another complicating factor is that the microflora present is utilizing, as well as producing, carbohydrate, and the fauna will be consuming some also. In any case my figures refer only to the simpler oligosaccharides present and not to the total carbohydrate content of the leaves; this is an important distinction.

MEIDELL: Have you analysed the faecal pellets to see which parts of the intake are utilized?

SAKWA: No—but I refer you to the paper by Bocock (1964)* which I have quoted.

* See list of references, p. 343.